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Community Ecology: Top-Down Turned Upside-Down

Within African savannas, elephants often damage individual trees to the extent that they influence tree density. New research shows that mutualistic ants inhabiting certain species of *Acacia* protect trees from catastrophic herbivory by elephants. Protection by the ants stabilizes tree cover across savannas in what is otherwise a highly dynamic biome.

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Biologists have debated about the ecological processes that regulate tree density in savannas for at least four decades [1,2]. Identifying the causal factors that determine whether a savanna is mostly grass or dense with trees has been elusive because savanna vegetation is often highly dynamic in space and time and the factors that regulate tree density are correlated in ways that can blur cause and effect [3]. Nonetheless, the implications of understanding the savanna biome are vital: savannas account for 20% of the earth's surface and support the majority of the world's rangeland and livestock. Moreover, a significant fraction of the global human population depends on savannas for their livelihood and welfare. Unfortunately, burgeoning human populations in and on the margins of savannas are threatening the stability of these ecosystems. Thus, solving the 'savanna problem' [4] is not only one of the more challenging issues facing ecologists, but also more pressing than ever before [5].

In general, explanations for the controls of tree density in savannas have focused on resources that limit tree growth (called bottom-up regulation), such as competition for water and soil nutrients, versus processes that cause mortality or consume biomass (called top-down regulation), such as browsing herbivores and fire [2]. A principal top-down control of tree density in African savannas is catastrophic herbivory by elephants (*Loxodonta africana*). Rather than gingerly plucking leaves and snipping branches like other African browsers, elephants often tear off large branches or knock down entire trees in order to forage. This foraging style, in combination with other factors such as fire, frost and disease [6–8], can convert woodland to open savanna. Elephant numbers have increased dramatically in many protected areas throughout Africa and, as a result, there is widespread concern and debate about the fate of mature woodlands and the capacity for trees to regenerate in the face of growing elephant populations [9,10].

As reported in this issue of *Current Biology*, Goheen and Palmer [11] demonstrate that a mutalistic relationship between an African ant (*Crematogaster* sp.) and the common whistling thorn Acacia (*Acacia drepanolobium*) turns what is typically a strong top-down effect of elephants on woodland biomass upside-down, thus contributing an important new piece to the savanna puzzle. The specifics of the ant–tree symbiosis are well known [12]: ants are provided with shelter and nutrition in the form of galls and extra-floral nectar from the trees, while trees are provided with defense from herbivory by the ants. What has not been clear, up until now, is just how effective these ants are at deterring megaherbivores and the landscape-scale implications of this mutualism. Goheen and Palmer's [11] findings show that these small soldiers are capable of protecting *A. drepanolobium* from the largest megaherbivore in Africa and essentially stabilizing tree cover across large areas in what is otherwise a highly dynamic biome.

Their approach was two-fold: in a first study, they analyzed tree cover at two separate areas in Kenya between 2003 and 2006; both areas contained fences constructed between 1992 and 2002 that excluded elephants. Moreover, elephant numbers were increasing sharply at both sites during the study period. High resolution satellite imagery showed that tree cover in woodlands dominated by ant-dwelling *A. drepanolobium* was unaffected by fences that excluded elephants. In contrast, tree cover in woodlands dominated by other tree species (i.e., those not inhabited by mutualistic ants) differed markedly inside and outside fences. Excluding elephants in these woodlands significantly increased the number of trees inside fences while trees remained at lower density outside fences, most likely due to elephant-caused mortality.

In a second study, they conducted a set of simple, but clever, experiments. A choice experiment with captive individuals convincingly demonstrated that elephants are quite capable of foraging on *A. drepanolobium* and do not discriminate against it once ants are removed. Moreover, when ants were experimentally added to *A. mellifera*, a tree preferably eaten by elephants, they avoided it during feeding trials the same way they avoided *A. drepanolobium* that contained ants. This pattern was then validated by evacuating ants from trees in the field using smoke and controlling the number of ants that recolonized the trees with sticky tape at the base of trees. The effect was an experimental manipulation of ant numbers on *A. drepanolobium* in the field that could be compared with elephant browsing. The results were simple and clear: elephant browsing was greater on trees with fewer ants and declined as ant numbers increased. Although elephants are the least prone of the megaherbivores to mortality by large mammalian predators [13] they are stopped in their tracks by the diminutive ant *Crematogaster*.

Will *A. drepanolobium* continue to expand its range across east African savannas if elephant numbers continue to increase? Not likely, due to the crucial twist that *A. drepanolobium* appears to be restricted to black cotton soils. Black cotton soils are vertisols, meaning they are composed of hydrophilic clay that expands when wet and contracts when dry, forming deep fissures and cracks. Although these soils are widespread in poorly draining regions throughout east Africa they are, with a few exceptions, not suitable for many tree species because they hold water very tightly and they cause severe mechanical damage to roots as they dry and crack. That *A. drepanolobium* is highly successful in black cotton soils but not in other soil types appears to be a significant evolutionary

tradeoff that may limit its future range. Whether or not the fidelity between *A. drepanolobium* and black-cotton soils is linked to the mutualistic relationship with the ants is unknown and will have to await further research.

One thing that is clear is that the stabilization of tree cover at the landscape-scale is associated with a series of processes that alter savanna functioning (Figure 1). First, in relatively large woodland patches, the accumulation of woody biomass can reduce the nutritive quality of the vegetation as forage for grazing herbivores [14]. Moreover, as trees provide good cover for predators, densely wooded savannas represent areas of relatively high predation risk for herbivores. As a result of the reduced forage quality and higher predation risk, except during long-distance movements or to obtain water, grazers tend to avoid areas with high tree density [15,16]. In turn, reduced herbivory can lead to the accumulation of herbaceous fuel loads, which is then associated with more frequent and severe fires [17]. This raises the interesting possibility that ant-derived protection from elephants may effectively switch the competitive and demographic controls over savanna function [18], from an herbivore-driven system to one driven by fire. As pointed out by Goheen and Palmer [11], the demographic controls over tree recruitment and mortality on the black cotton soils are more likely to be related to fire and water availability than regulation by herbivores. In summary, this article demonstrates that a single plant–insect mutualism can have profound effects on savanna structure and function. Moreover, their research provides compelling evidence that the processes regulating savanna tree demography and ecosystem function within savannas may depend strongly on soil type. While many individual pieces are still missing, with the contribution of Goheen and Palmer [11] the savanna puzzle is more manifest than ever.

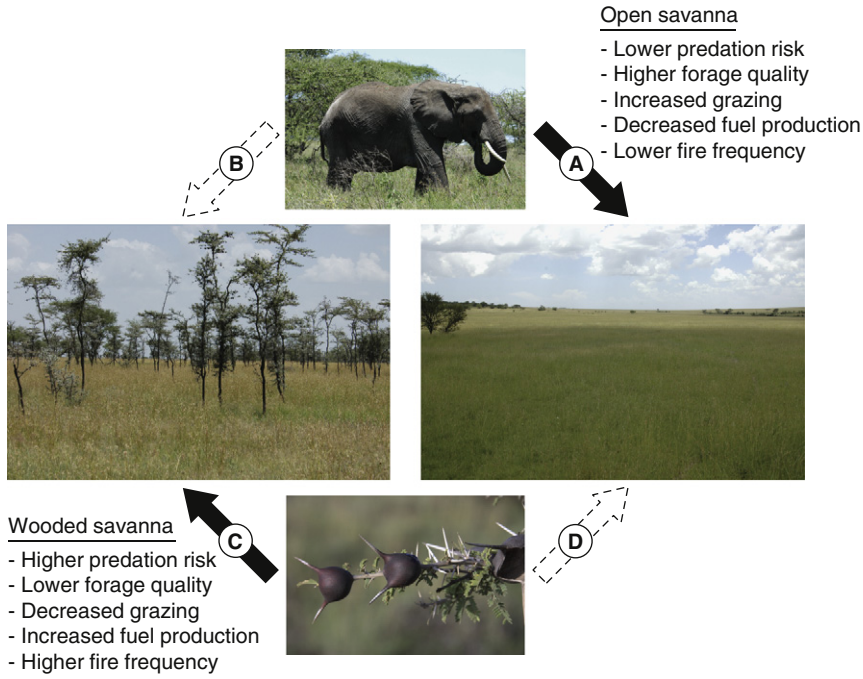

Figure 1. Landscape implications of an ant–Acacia mutualism in African savannas.

Elephants typically exert strong top-down control of tree density in African savannas (arrow A). In their report, Goheen and Palmer [11] show that this relationship is disrupted (arrow B) by the symbiotic relationship between the African ant *Crematogaster* and its mutualistic host the whistle thorn Acacia (*A. drepanolobium*). This mutualism effectively stabilizes tree cover on black-cotton soils where *A. drepanolobium* dominates (arrow C) while tree dynamics persist in other soil types (arrow D). One spin-off effect of the mutualism may include a switch in the dominant drivers of savanna function, specifically, between savannas regulated by either herbivory (open savannas) or fire (wooded savannas).

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